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ORIGIN OF SINGLE CHARACTERS AS OBSERVED IN FOSSIL AND LIVING ANIMALS AND PLANTS¹

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IN the last thirty years two biologies have been developing. The first is the biology of the garden, the seed pan, the incubator, and the breeding pen. The second is the biology of the field zoologist, of the field botanist, of the paleontologist. Inasmuch as one regards unnatural processes and the other regards natural processes it is small wonder that these biologies have become as far apart as two religions and have developed their sects and their dogmatists. Yet the actual *facts* assembled in these two biologies as distinguished from the *opinions* based thereupon can not be in the least discordant, for certainly there is only one system of law operating in the living world and there can be only one ultimate and final biology. In my Harvey lecture of 1912² the search for some unity between the observations in these two great fields of natural and experimental research met with some failure

¹ Presidential address before The Paleontological Society of America, delivered in the Academy of Natural Sciences of Philadelphia, Wednesday, December 31, 1914.

² The present address, as a comparison of zoological, paleontological, and experimental results, is a sequel to the author's Harvey Lecture of 1912, entitled "The Continuous Origin of Certain Unit Characters as Observed by a Paleontologist." Harvey Soc. Vol., 7th ser., Nov., 1912, pp. 153-204. It employs in part the same materials and illustrations.

and some success, and in the present address I am pushing inquiry along the same line, choosing the "single character" as the point of investigation and comparison.

THE ORIGIN OF CHARACTERS

The old and ever vague problem of the origin of species is being resolved into the newer and more definite problem of the origin of characters; in the dim future when we know how and why new characters originate, and how and why they transform and disappear, the problem of natural and experimental research met with some failure and some success, and in the present address I am pushing inquiry along the same line, choosing the "single character" as the point of investigation and comparison.

THE ORIGIN OF CHARACTERS

The old and ever vague problem of the origin of species is being resolved into the newer and more definite problem of the origin of characters; in the dim future when we know how and why new characters originate, and how and why they transform and disappear, the problem of species will have long been solved and well-nigh forgotten. This is because a species is an assemblage or colony of similar individuals, each individual is composed of a vast number of somewhat similar new or old characters, each character has its independent and separate history, each character is in a certain stage of evolution, each character is correlated with the other characters of the individual.

Thus in a sense the species, the subspecies, the variety, even the individual is not a zoological unit, whereas the "character" when narrowed down to the last point of divisibility seems to be a unit both among plants and animals, and a very stable one, with certain distinctive powers, properties, and qualities of its own. We have been approaching this new conception from many different lines of observation among fossil and living animals and plants, and a preliminary survey of results is opportune.

My chief purpose in this address is to show what one of these "single" or "least characters"³ is and what peculiar powers and properties it possesses which distinguish it from other "least characters" and give it a certain individuality and separateness.

If you read your Lamarck, your Darwin, your Cope afresh with this general conception in mind you will find that throughout biological literature the problem of species has always been an incidental one, a sort of by-product and relic of the very ancient controversy as to whether species were created suddenly or evolved gradually. The real problem has always been that of the origin and development of characters. Since the "Origin of Species" appeared the terms variation and variability have always referred to single characters; if a species is said to be variable we mean that a considerable number of the single characters or groups of characters of which it is composed are variable. In botany the long overlooked discovery of Gregor Mendel in 1865 had as its most essential feature the separability of characters in heredity. In paleontology as long ago as 1869 Waagen sharply focused our attention on single phyletic characters as of far greater significance and importance than the matter of local races, varieties, and subspecies. The modern observers in experimental zoology and heredity are far less concerned with "species" than with the separate characters of which the individuals within a species are composed.

Some naturalists incline to regard the "character" as observable only by certain methods of their own, but it is obvious that since all hereditary "characters" are germinal there can be no royal or exclusive road by which we may observe their origin and transformation, for the germinal and somatic laws controlling the characters of

³ T. H. Morgan has pointed out that the term "unit character" was improperly used in my Harvey address. "Unit character" is a germinal rather than a bodily term. I am treating here of single bodily or somatic characters which may be represented by one or more "unit characters" in the germ.

the bean,⁴ the fly,⁵ the mollusc,⁶ the titanothera,⁷ and man⁸ are doubtless identical.

Accordingly my second purpose in this address is to show that there is a certain harmony in the results obtained in widely different fields of research although some of these results may appear at first to be entirely unrelated and even discordant.

In this attempt to discover an underlying harmony let us first glance at the "character" conception in the older natural sciences of animals and plants. CHARACTER is the most frequently used term in the vocabulary of zoology and botany. It occurs far more often than any other word. It has been used millions of times in systematic definition since Linnæus. Yet I do not know of any attempt to clearly define or analyze the meaning of the word character in its biologic sense while hundreds of attempts have been made to define the word species. Here again the greater is involved in the less and whenever we shall succeed in clearly defining "character" the definition of species will follow as an incidental result.

The derivation of the word is from the Greek *χαρακτήρ* properly an instrument for marking or graving; as applied to a person, an engraver; as commonly used, any mark engraved or impressed, the impress or stamp on coins and seals. It passes into the word characteristic, which means a distinguishing feature.

The use of the word is not only universal among systematists and experimentalists of our day, but it has become one of the most elastic words in our language; the "character" may be as comprehensive as the general habit of an entire organism, as where we speak of the lethargic character of the sloth, or as restricted as a single minute cuspule on a fossil tooth, or the barely visible outgrowth on the surface of a fossil shell. The speed of the race horse is a character, its tractability or viciousness are characters, the position of the horse's tail in running

⁴ Johannsen.

⁷ Osborn.

⁵ Morgan.

⁸ Galton.

⁶ Waagen, Neumayr, Hyatt, Jackson.

is a character, the color of the horse's hair is a character, the most minute cellular structure of the tissue of the hoof is a character.

There is an underlying reason why this very elastic use of the term is absolutely scientific: it is, that every one of the above diverse applications of the term to animal or plant life refers to some structure or some quality which is *heritable*; heredity is the unifying principle.

The word is again elastic and often confusing in being used both for germinal characters which are always heritable and for bodily modifications of character acquired through habit or environment which may not be heritable. When we speak of characters which are not known to be hereditary we should qualify them as acquired, as modified, as due to nurture, to habit or ontogeny, to environment, as somatic rather than as germinal. Thus it is perfectly proper to speak of "ontogenetic species" as Jordan does, species the bodily characters of which are due to certain habits; or of "environmental species" the bodily characters of which are due to peculiarities of environment. While such modifications by habit and by environment make up a considerable part of the characters which distinguish geographic species, subspecies and races, it is not the origin and the transformation of these characters which we are now considering, for that problem is comparatively simple, but rather of those underlying *germinal* and *heritable characters* the origin and transformation of which is absolutely an impenetrable mystery at the present time.

How do we know through zoology, botany, and paleontology as well as through experiment that "characters" are real units of structure with some individual and distinct qualities and properties of their own which separate them from all their fellows and at the same time with certain properties of correlation which unite them with all their fellows?

First, we may observe in these living and extinct forms evidences of two such antithetic principles, a principle

of *hereditary separability* whereby the body is a colony, a mosaic of single individual and separable characters, which is combined with a principle of *hereditary correlation* whereby the body is a complex of minutely related and interacting units so that functionally and structurally many of these units are linked with others. Neither principle is simple; on the contrary, both principles are extraordinarily complex and go back to the very beginning of things. Comparing more closely the observations on fossil vertebrates and invertebrates, we develop *laws of separability* as well as *laws of correlation*, and note that certain of these laws are far more clearly perceived in some fields of observation than in others.

The biologic value of the field to which our Paleontological Society is especially devoted lies in the revelation of certain of these laws and causes of the separability of characters which are not revealed at all to the zoologist or to the experimentalist. The paleontologist is in a position to understand *why* certain characters fall apart and become separable in cross breeding, the cause being connected with their origin and antecedent history.

Of far broader biologic significance is the fact that all principles which may be discovered through paleontology regarding the "origin of characters" in the hard parts, govern alike characters of the soft parts as well as of other structures and functions. For there can not be one principle governing the "characters" of bones, another those of the muscles, another those of nerves; one principle for structures, another for functions. But while these principles are unlimited, our *comparisons* with zoology, for example, are limited to the origins of characters which may be observed both in living and fossil forms, namely, in the skeleton and in the teeth; and at the outset a convenient and readily understood distinction may be made between the origins of *numerical* and of *proportional* characters, as follows:

Numerical

Presence and absence characters, *e. g.*, numbers of teeth, of cusps on the teeth, of vertebræ, of toes, of pads on the feet, of mammæ. Meristic or segmental characters, such as may be partly expressed in *formulae*.

Proportional

Changes of form in the length, breadth and height of parts. Quantitative changes in the hard parts. Such characters as may partly be expressed in *indices* and *ratios*.

Proportional characters may through prolonged reduction lead into numerical characters. Thus the reduction in length of one of the toes may precede the loss of the toe, which is a numerical change. Yet we shall see that somewhat different principles prevail in the origins of certain numerical characters as contrasted with the origins of proportional characters.

1. *Use of Numerical and Proportional "Characters" in Classification of Mammals*

In our attempt to analyze "characters" as they are revealed to the systematic and field zoologist let us take as two examples, first, "The Catalogue of the Mammals of Western Europe" by Gerrit S. Miller,⁹ and, second, the "Revision of the Mice of the genus *Peromyscus*," by Wilfred H. Osgood. It is of the utmost importance that mammalogists, whether working among living or fossil forms, should use similar methods of description and definition of characters, and we especially welcome in the monumental work of Miller the fact that the definitions and the keys are chiefly upon the hard parts which are also available to the paleontologist. We select as typical his treatment of the Order Carnivora and of the Family and Genera of the wolves and foxes, which he distinguishes by the following enumeration of characters:

<i>Miller's</i> <i>Diagnoses and Definitions</i>	<i>Our Analysis of the Kinds of</i> <i>Characters</i>
ORDER CARNIVORA. <i>Characters</i> . —Terrestrial (rarely aquatic or	Chief habits, chief adaptations of the teeth and limbs; chief char-

⁹ Miller, Gerrit S., "Catalogue of the Mammals of Western Europe (Europe exclusive of Russia) in the Collection of the British Museum." London, 1912, 1019 pp.

semi-aquatic), non-volant, placental mammals with rather high development of brain. The cerebral hemispheres with distinct convolutions; feet unguiculate, never modified as fins or flippers; dentition of a modified tuberculo-sectorial type, the posterior upper premolar and anterior lower molar usually developed as special carnassial or flesh-cutting teeth.

Family CANIDÆ. *Characters*.—Larger cheek-teeth of a combined trenchant and crushing type, the last upper premolar and first lower molar strongly differentiated as carnassials, the former 3-rooted, its inner lobe in front of middle of crown, its position, somewhat posterior to level of anteorbital foramen, at point of greatest mechanical efficiency; auditory bulla moderately or considerably inflated, without septum; form rather light, the legs long; size moderate; feet digitigrade; toes, 5-4 or 4-4.

Genus CANIS. *Characters*.—Skull heavy and deep (depth of brain-case more than one-third condylobasal length); interorbital region thickened and elevated, the frontal sinuses rather large, the postorbital processes thick, convex above, their edges rounded off; dorsal profile of forehead rising rather abruptly and noticeably above level of rostrum; dental formula;

$$i \frac{3-3}{3-3}, c \frac{1-1}{1-1}, pm \frac{4-4}{4-4}, m \frac{2-2}{3-3} = 42;$$

teeth heavy and large, the length of carnassial and upper molars together contained about $2\frac{1}{2}$ times

acters of the brain. Inherited from "least characters" which accumulated and evolved in Mesozoic and early Tertiary time.

Characters of proportion and changes of form; characters of function or adaptation; presence or absence of certain numerical characters. Characters by which the ancestors of the family diverged as terrestrial and cursorial Carnivora from other Carnivora.

Chiefly characters of proportion; also numerical characters of the teeth. Characters clearly manifested in lower and middle Eocene time and taking on their modern aspect in early Oligocene time.

in palatal length; canines robust and not specially elongated, the point of upper tooth extending scarcely beyond middle of mandibular ramus when jaws are closed (Fig. 65).

[Species] *CANIS LUPUS*. *Diagnosis*.—Condylobasal length of skull more than 200 mm. (220 to 225 mm.); cheek-teeth larger than in the largest races of domestic dogs, the upper carnassial 25 to 27 mm. in length, but structure not peculiar, the upper molars with narrow, inconspicuous cingulum on outer side (Fig. 61).

[Subspecies] *CANIS LUPUS LUPUS*. *Characters*.—Size maximum for the species; general colour not markedly tawny; white of throat not extending to cheeks. The few skulls examined agree with Asiatic specimens in having the outer cusps of m^1 moderately large, the paracone with transverse diameter of base about equal to width of large flattened portion of crown.

Chiefly characters of proportion; certain minor numerical characters. Characters distinguishing *Canis lupus* from *Vulpes*, first apparent in Miocene and Pliocene time.

Size characters; color characters; proportions of dental cusp characters. Characters fully developed in early Pleistocene time, perhaps 500,000 years ago.

In the ascending order of Miller's definitions we note that "subspecies are mainly distinguished by characters of proportion and of form and by the degrees and intensities of color, but rarely if ever by numerical characters. "Species" are mainly distinguished by the proportions of the various hard parts and to a less extent by the presence and absence of minor "numerical" characters. "Genera" are distinguished by the proportions, by the presence or absence of several numerical characters, also by functional characters such as dental succession. "Families" are distinguished by changes of proportion and of form, by many numerical characters, such as the presence or absence of certain parts, by structural adaptations in the teeth and feet. "Orders" are distinguished by the funda-

mental and very ancient chief habits, chief adaptations in the hard parts, chief brain features.

Thus we see that two kinds of characters are employed by Miller throughout, namely: first, characters of proportion of form and of degree; second, numerical or

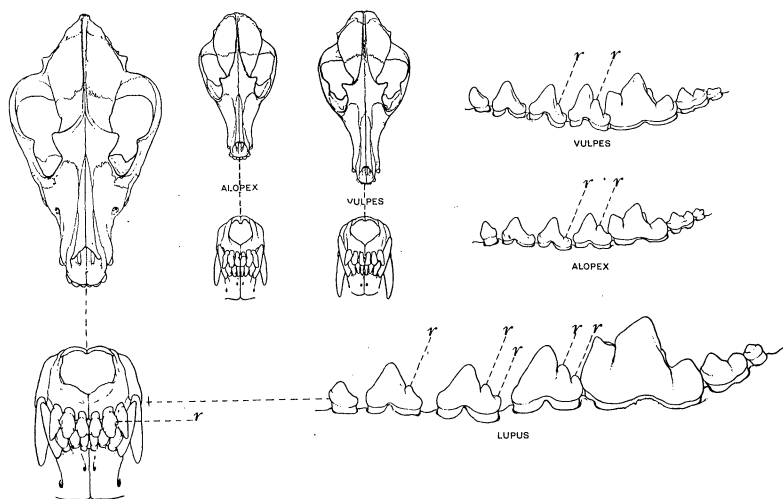


FIG. 1. Skulls and cheek teeth of the wolf (*Lupus*), arctic fox (*Alopex*), and red fox (*Vulpes*), illustrating the differences in proportional characters of the skulls and teeth and the resemblances in the numerical characters, or rectifications (*R*).

presence and absence characters. We are struck by the fact that changes in proportion embrace by far the larger part, perhaps nine tenths, of the "characters" enumerated by Miller in his systematic descriptions; this is because *change of proportion is the chief and most universal phenomenon in the adaptation of mammals to different habits and habitats. Numerical change is hardly less important, but is less universal and less frequent.*

Similar weight upon the value of characters of proportion is seen in the contrast between Miller's definitions of the three genera of dogs, namely: *Canis*, *Alopex*, and *Vulpes*. Here again the vast majority are characters of proportion and of form.

I. Genus *CANIS*

Characters. — Skull heavy and deep (depth of brain-case more than one-third condylobasal length); interorbital region thickened and elevated, the frontal sinuses rather large, the postorbital processes thick, convex above, their edges rounded off; dorsal profile of forehead rising rather abruptly and noticeably above level of rostrum; dental formula:

$$\begin{array}{c} 3-3, \quad c \frac{1-1}{1-1}, \quad pm \frac{4-4}{4-4}, \\ m \frac{2-2}{3-3} = 42; \end{array}$$

teeth heavy and large, the length of carnassial and upper molars together contained about $2\frac{1}{2}$ times in palatal length; canines robust and not specially elongated, the point of upper tooth extending scarcely beyond middle of mandibular ramus when jaws are closed (Fig. 65).

II. Genus *ALOPEX*

Characters. — Skull intermediate in general form between that of *Canis* and *Vulpes*; occipital depth about one-third condylobasal length; interorbital region more elevated than in *Vulpes* owing to greater inflation of the frontal sinuses; postorbital processes thin, flat or slightly concave above, with bead-like, overhanging edges; dorsal profile of forehead rising abruptly above rostrum as in *Canis*; teeth moderately heavy and large, the length of carnassial and upper molars together contained about $2\frac{3}{4}$ times in palatal length; canines and incisors intermediate between those of *Canis* and *Vulpes* (see Fig. 65); external form fox-like, but ear short and rounded, not conspicuously overtopping the surrounding fur.

III. Genus *VULPES*

Characters. — Skull slender and low (depth of brain-case less than one third condylobasal length); interorbital region nearly flat, the frontal sinuses scarcely inflated, the postorbital processes thin, slightly concave above, their edges overhanging and bead-like; dorsal profile of forehead rising very slightly and gradually above level of rostrum; dental formula as in *Canis*; teeth relatively light and small, the length of upper carnassial and molars together contained about $2\frac{3}{4}$ to 3 times in palatal length, the general character of cheek-teeth somewhat more trenchant than in *Canis*, the canines slender and elongated, the point of upper tooth extending to about lower margin of mandibular ramus when jaws are closed (Fig. 65).

The fact that changes of proportion include the most frequent characters while numerical changes include the least frequent characters is again very strikingly brought out in Miller's remarks on the origin of the domestic dogs from the wolf (*Canis lupus*):

The only known characters by which the skull of *Canis lupus* can be distinguished from that of the larger domestic dogs is the greater average general size and the relatively larger teeth. In a dog's skull with condylobasal length of 230 mm. the length of upper and lower carnassials is, respectively, 21.6 and 25.0 mm. In ten skulls with condylobasal length of more than 200 mm. the average and extremes for these teeth are: upper, 20.5 (19-22); lower, 24.0 (22.8-26.0). In all the dog skulls which I have examined, representing such different breeds as the pug, fox-terrier, bloodhound, mastiff, ancient Egyptian, ancient Peruvian, Eskimo (Greenland and Alaska) and American Indian, the teeth are strictly of the wolf type, never showing any approach to that of the jackal (Fig. 62).

This indicates that the profound differences of osteological character which separate the larger breeds of domestic dogs are chiefly in the proportions.

No numerical, or presence and absence characters are used in Miller's definition of the wolf, arctic fox, and red fox although a number of minor numerical characters are clearly described and figured in his text, especially the cuspules on the incisor and premolar teeth, as shown in Fig. 1. These numerical cusp characters would have received more attention from a paleontologist partly because of the paucity of material which comes into his hands, partly because he is in a position to observe the development of these cuspules.

This contrast between proportional and numerical characters brings out a fundamental law in the evolution of the hard parts of mammals which is of great importance. First, characters of form and proportion, without numerical change, are constantly originating as a universal principle and forming the chief distinctions between divisions from the high rank of orders down to those of subspecies, races, and even individuals. Second, numerical loss or fusion of old characters of teeth, digits, or vertebræ is next in frequency, the loss always following diminution in form and proportion. Third, numerical gain of new characters is the least frequent process; it is relatively rare in the endoskeleton, that is, in added teeth, added vertebræ and other segmental parts, added cranial bones, added phalanges; it is more frequent in added cusps on

the teeth or added horns and appendages of the skull; it is still more frequent in added exoskeletal characters, such as dermal ossicles and armatures.

The contrast between the wolf (*Canis lupus*), the arctic

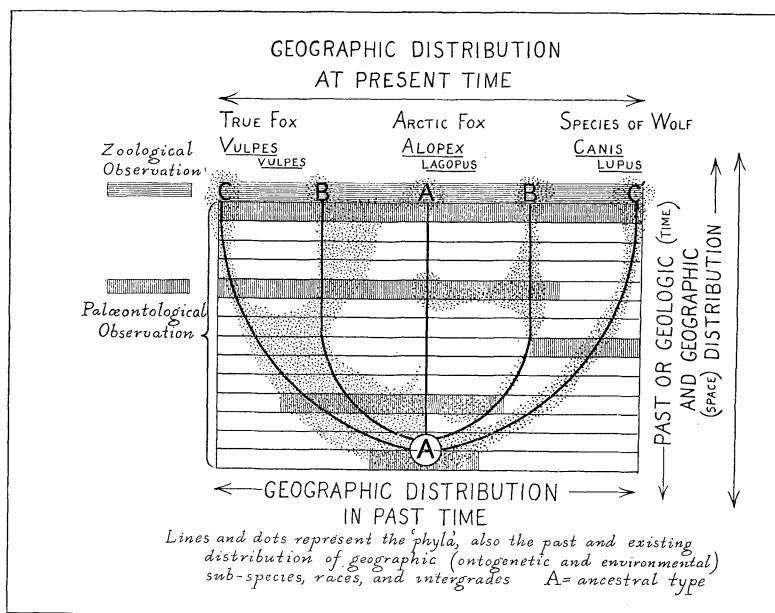


FIG. 2. Diagram illustrating the theoretic descent of the dogs from a common geologic ancestor A. Dots = intergradations observed by the paleontologist (vertical lines) at five different intervals of geologic time. A B C = existing forms with a few existing intergradations (dots) observed by the zoologist (horizontal lines).

fox (*Alopex lagopus*), and the red fox (*Vulpes vulpes*) may, moreover, be adduced for four purposes: first, to direct attention to the nature of the *numerical characters* which separate these three genera; second, to direct attention to the fact that these numerical characters are very inconspicuous and unimportant in contrast with characters of proportion; third, to illustrate the extremely slow development in time of new numerical characters; fourth, to illustrate the difference between paleontological and zoological observation, a difference which is graphically represented in the diagram (Fig. 2).

As to time *Vulpes* has been separated from *Canis* for an

enormous period.¹⁰ It is clearly distinguishable in the European Pliocene where three species of canids are referred to the genus *Vulpes* by Schlosser and others. Again, in the Upper Pliocene of India there occurs a species of fox as well as in the Pliocene of China. In North America the fox is first recorded from the Pleistocene definitely, although an Upper Miocene species (*Canis vafer* Leidy) is regarded by some as the forerunner of *Vulpes* and by others as a pro-*Vulpes* genus. It is therefore probable that the phylum of the fox diverged from that of the wolf as early as Miocene times, perhaps a million years ago, although the generic distinctions of proportion-characters were not fully acquired until Pliocene times. The ancient geologic separation of *Canis* and *Vulpes* is further indicated by the fact that they do not interbreed. The marked divergence in proportions—the fox small, slender, narrow-headed, a small-mammal and bird catcher, the wolf relatively large, massive, broad-headed, a large-mammal catcher—is accompanied by the gain or loss of several *relatively obscure* numerical characters, such as the cuspules on the incisors and premolars (Fig. 1. *r, r, r*), which are strong in the wolf, intermediate in the arctic fox, and absent in the red fox. It would appear that the wolf had developed these numerical cusp characters more rapidly than its congeners. In a fossil series the development of such cusp characters may be followed stage by stage.

2. *Observations by a Field Zoologist on the Modes of Origin of Numerical and Proportional Characters*

The special features of the field work developed under C. Hart Merriam's direction in the U. S. Biological Survey are: (1) the vast quantity of comparative material brought under examination, (2) the exact geographic, climatic and environmental records, (3) the assemblage of numerous intergradations between species and sub-species, (4) the precision of the measurements and observa-

¹⁰ I am indebted to the authority of Dr. W. D. Matthew for these remarks.

tions, but above all (5) that the *facts are recorded entirely without the influence of any biological theory*, the mind of the observer being absolutely fresh and unprejudiced.

The observations published in 1909 by Wilfred H. Osgood on the mice of the genus *Peromyscus*¹¹ therefore constitute a notable and wholly unbiased research on bodily "characters" as they appear to a zoologist collecting and observing in the field, but examining and reviewing his material in the museum. The following abstract is mainly in the author's own language and has been verified by him, although the order of treatment is rearranged entirely and italics are added for emphasis in its bearing upon the modes of origin of single characters in living mammals.

As recorded there have been examined more than 27,000 specimens of the American rodent genus *Peromyscus* (Gloger, 1841), including the so-called wood mice, deer mice, vesper mice, or white-footed mice, having a total range from the Mexican province of Oaxaca on the south to the Yukon, Alaska, on the north, and from Labrador to Florida on the east to Alaska and southern California on the west.

The "genus" *Peromyscus* is for convenience divided into five "subgenera," which are distinguished mainly by the presence or absence of three *numerical* characters, namely, tubercles on the soles of the feet five or six, presence or absence of accessory tubercles on the first and second molar teeth, presence or absence of two or three pairs of mammae. The remaining subgeneric characters lie in *differences of proportion* and in *color relations*. The "subgenera," which are usually defined by a combination of characters, may merely represent *opposite ends of an almost continuous series* (e. g., *Haplomylomys-Peromyscus-Megadontomys*). Intergradation is observed also in certain of the numerical characters, as in the six to vestigial five plantar tubercles of the *P. maniculatus* group.

The species of *Peromyscus maniculatus* (Wagner), alone including forty-four subspecies, ranges from Vera Cruz to Labrador and has a wider distribution and a larger number of intergrading forms than any similar group of mammals known. From the typical *P. maniculatus* *development may be traced step by step absolutely without break through all the numerous subspecies*.

Perfect intergradation, in proportion and color intensity and distribution characters, is observed between the related forms ("sub-

¹¹ Osgood, Wilfred H., "Revision of the Mice of the American Genus *Peromyscus*," U. S. Dept. of Agric., Bureau of Biol. Surv. No. Amer. Fauna, No. 28. Apr. 17, 1909, 285 pp.

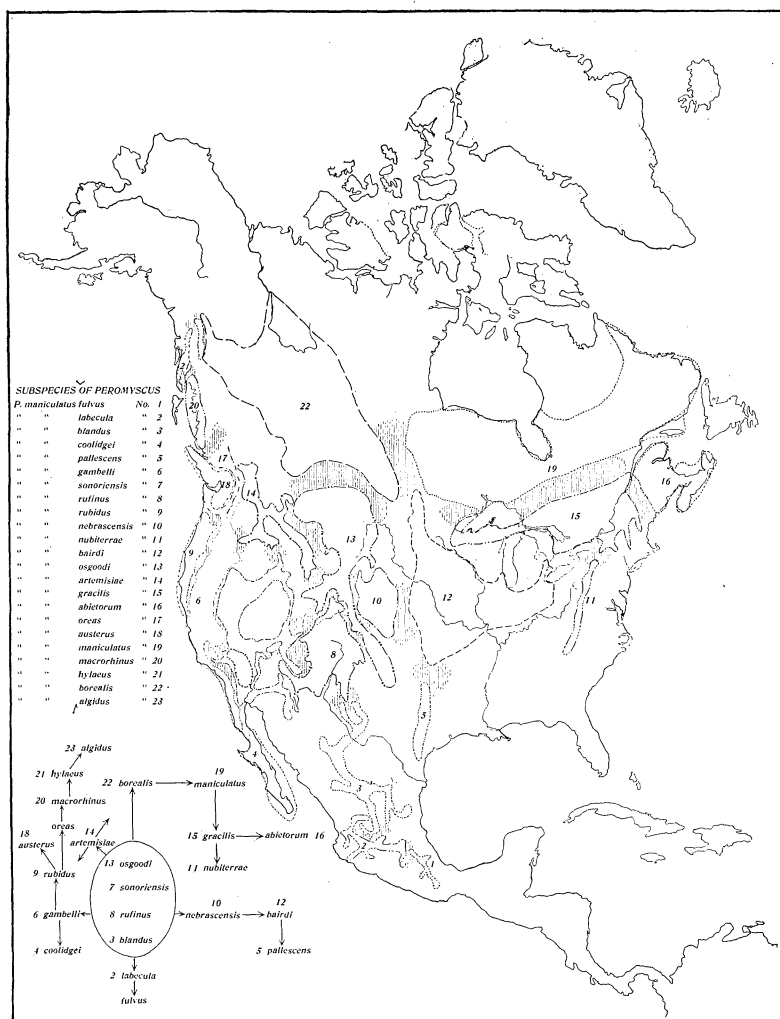


FIG. 3. Geographic distribution of the subspecies of *Peromyscus maniculatus*. The geographic boundaries of each subspecies are represented by continuous or variously dotted lines. The areas of complete intergradation or continuity between two subspecies are indicated by vertical shading. Where there is no shading there is an apparent discontinuity which, as indicated in the diagram in the lower left-hand corner, is not real; this diagram shows the various continuous chains of subspecies and intergradations the terminal members of which appear to be discontinuous.

species") of the many different faunal areas. Hundreds and even thousands of specimens are intergrades almost equally resembling two or more adjacent forms. Many specimens fall so near an imaginary line between two or more "subspecies" that it is practically impossible

to classify them other than as intergrades. Particularly difficult cases are those in which the intergrades approximate the color of one "subspecies" and the cranial characters of another, thus reducing the question of definition to one of the relative importance of characters. Classification becomes like the division of a spectrum and depends largely upon the standards set, for theoretically at least the possibilities of subdivisions are unlimited.

Some of the principles of variation [and perhaps of hybridization, H. F. O.] are as follows:

(1) Fortuitous individual variation is greatest in specimens from localities lying just between the ranges of two well-established forms.

(2) Where two genuine "subspecies" inhabit the same area and maintain themselves distinct, each may in certain cases be traced by a definite geographic route through every degree of intergradation to one parent form. For example, *P. arcticus* lives side by side with *P. algidus* in the upper Yukon, but both intergrade toward the south with *P. oreas* (see Fig. 3). If from sudden or gradual natural causes these intergrades between *P. arcticus*, *P. oreas*, and *P. algidus* were to become extinct three entirely separate and distinct subspecies would apparently be created.

(3) Sexual variation in proportional characters is so slight as to be practically unmeasurable.

(4) The "species" are fairly well characterized in cranial proportions, but the cranial proportions in "subspecies" are seldom constant throughout a series although they often afford average proportional characters of considerable value. For example, among "species" that are normally brachycephalic a greater or less tendency to dolichocephaly is sometimes found, and *vice versa*. The teeth vary chiefly in proportions but seldom to great extent. Some subspecies are dichromatic.

(5) In color there is a range of seasonal, polychromatic, and local or geographic variation. A complete intergradation between two color extremes may often be found in localities lying just between the ranges of two well-established forms. Color intensities are often extremely local and doubtless are produced immediately upon contact with certain environments. Thus if the range of a given subspecies includes a few square miles of lava beds, specimens from that area show appreciably darker color than the normal members of the subspecies occupying the surrounding region. Again, specimens from the bottom of a dark, wooded cañon may be noticeably darker than those inhabiting an open hillside only a few hundred yards away. One can hardly avoid the suspicion, observes Osgood, that if the progeny of paler individuals were transferred at an early age to the habitat of the darker ones they would quite regardless of heredity develop darker color. Such local "geographic variations" are so great that most of the species have developed geographic peculiarities by means of which

they have been subdivided into numerous "geographic races" and "subspecies." Thus *P. maniculatus*, which ranges from the Arctic Circle to the Isthmus of Tehuantepec, remains constant only where the environment is identical, hence it is represented by definable "subspecies" in almost every faunal area which it enters (see Fig. 3).

These observations of Osgood may be compared with the taxonomic results of Miller on the one hand and with the observations of paleontologists on the other:

First: we note that in the "species" of the subgenus *Peromyscus* and in the "subspecies" of *Peromyscus maniculatus* among the vast number of characters enumerated there is not a single distinction recorded in numerical or presence and absence characters; every single character recorded is either in the proportions of the skull, ears, feet, and tail, or in the intensities and distribution of the color areas—all characters of degree. The field and museum work of Osgood thus independently accords with the taxonomic work of Miller, namely, "proportional characters" are universal and abundant, "numerical characters" are less frequent and of a higher or different taxonomic order because much more gradual in evolution.

Second: *the evidence for continuity in the origin of proportional characters is absolute.*

Third: in a broad way *continuity is also the mode of origin of the so-called numerical characters* for it is positively observed except in the case of the mammæ, and there is no apparent reason, remarks Osgood, why the mammæ also may not have developed in the same way as the more trivial characters. In other words, there is almost complete continuity between groups which many taxonomists would regard as different "genera." The numerical differences in the plantar tubercles on the soles of the feet have not been sufficiently studied, but it is clear that the change from 5 to 6, or *vice versa*, has come through the gradual reduction or growth of one tubercle and not through any sudden change. Most interesting also is the fact that the 5-tubercled *Peromyscus* shows decided similarity to the genus *Onychomys*, which is 4-tubercled and closely allied to *Peromyscus*.

Fourth: while the numerical characters are solely germinal, it is difficult or impossible to distinguish both in respect to color intensities and to proportions, what is germinal, permanent and hereditary from what is somatic or due to environmental and ontogenetic influences.

These four chief conclusions drawn from the observations of Osgood may now be compared with those independently obtained by paleontologists.

3. *Likeness and Unlikeness Between Paleontologic and Zoologic Observation*

The mammalian paleontologist observes exactly the same *kinds* and *degrees* of characters as the zoologist, namely, very numerous changes of proportion and form, and relatively infrequent numerical changes. In both respects, however, the paleontologist has the very great advantage of observing the extremes and also many of the intermediate stages.

The chief distinction between these observers is that as the zoologist sees characters they are stationary, he can only infer their separability in movement through his inferences from the comparison of forms like *Canis*, *Alopex*, and *Vulpes*, while the paleontologist observes several new evolution properties in these same "characters," namely their actual *movement* and their relative *rate of movement* in various lines of descent, as well as their *origin* and subsequent progression or retrogression, in brief, their *phyletic history*. Thus the paleontologist is in a position to observe more of the evolution properties in characters of exactly the same kind. Whereas in a series of living forms each character appears to the zoologist-observer as dead or static, in a fossil series each character appears to the paleontologist-observer as living or dynamic, the life being displayed in what may be called its two *movements in a phyletic series*.

The first property of the *ontogenetic movement* of characters in fossils constituted the life work of our great observer Alpheus Hyatt, who proposed the significant and easily recalled terms *acceleration* and *retardation* for the

two directions of movement seen in ontogeny and phylogeny. Accelerated characters are those which hurry forward and appear in successive generations at earlier and earlier stages in the development of the individual; while retarded characters are those which hold back or slow down and appear in later and still later stages in the development of the individual of succeeding generations. We know that such ontogenetic movement is shown both in embryonic and phylogenic development of the individual; it causes characters to appear in ontogeny out of the order in which they arise in phylogeny; it gives rise to the heterochrony of Gegenbaur; its rate is measured by comparing one character with all the other characters of an individual.

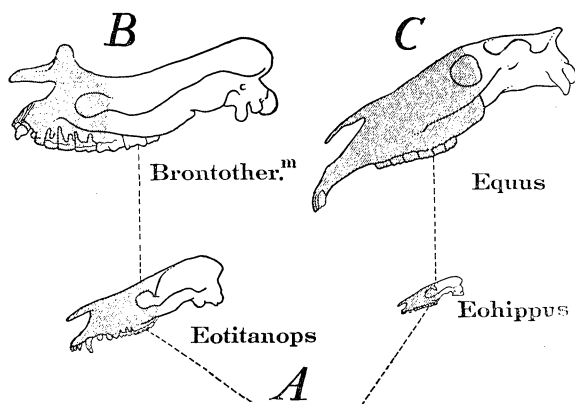


FIG. 4. Evolution of profoundly different proportional characters (B, C) from ancestors (A) having similar proportions.

Quite distinct is what we may call the *phyletic movement* of a character; its rate is measured by comparing a character in individuals of one phylum with the same character in individuals of other phyla. It is illustrated in the comparison of the secondary cusps of the incisor and premolar teeth in *Canis*, *Alopex* and *Vulpes*; in each phylum the same cusp has its distinctive rate of evolution and thus may appear early in geologic time or late in geologic time. Thus comparison of the phyletic movement of the same "character" in various lines of descent,

which is a matter of phylogeny, is quite different from comparison of the relative movement of a number of different characters in single lines of descent, which is the basis of Hyatt's law.

To illustrate the distinction between ontogenetic and phyletic movement: a rudiment of a horn may appear upon the skull in one phylum of titanotheres during the period of deposit of the base of the Bridger beds (Fig. 5), which are 1,500 feet in thickness, and in another phylum (Fig. 5) at the summit of these beds, many thousands of years later; this is its relative *phyletic movement*. Second, after the same horn-character has appeared long subsequent to the birth of the individuals, in both phyla it begins to be thrust forward in the ontogeny of individuals, so that in Lower Oligocene time it begins to appear long before birth; this is its acceleration or *ontogenetic movement*.

Paleontology has also revealed the marked distinction in the mode of origin of the two kinds of characters observed in zoology, namely, between the almost universal changes of proportion and the comparatively rare new "numerical characters."¹²

To the former I have applied the term *allometrons*,¹³ which signifies that differences of measurement express all changes of proportion. From these differences indices and ratios may be calculated. Such differences arising in the head and in the feet are indicated in the familiar terms dolichocephaly, brachycephaly, dolichopody, brachypody, and many other convenient combinations of Greek terms. That these changes of proportion become distinct hereditary "characters" is proved in certain hybrids of mammals where they appear to be partly or completely separable. Thus the cross of human broad-heads with long-heads does not produce a blend between the two but produces, for some generations at least, either pure doli-

¹² Osborn, H. F., "Coincident Evolution Through Rectigradations (Third Paper)," *Science*, N. S., Vol. XXVII, No. 697, May 8, 1908, pp. 749-752 (p. 752).

¹³ "Biological Conclusions Drawn from the Study of the Titanotheres," *Science*, N. S., No. 856, May 26, 1911, pp. 825-828 (p. 826).

chocephals or pure brachycephals. Characters of proportion are thus "single characters" in the hereditary sense.

In the comparison, for example, of certain broad-heads with other broad-heads such characters are termed *analogous* because due to similarity of structure arising from similarity of function. Thus brachypody (abbreviation of the digits) is analogous in the rhinoceroses and the titanotheres. The broadening of the shell of one mollusc is analogous to the broadening of the shell of another mollusc. The broadening is none the less the heritable characteristic of the skull or of the shell.

Quite different are certain of the new numerical characters to which I have applied the term *rectigradations*,¹² such as new cuspsules on the teeth and new rudiments of horns, for these give rise to characters which are regarded as *homologous* although not directly descended from each other. Thus the horns in all the titanotheres are considered homologous, although they arise independently at different times in different phyla. The larger number of cusps in the teeth of mammals are termed homologous, although they also have arisen quite independently of each other. It is obvious that unless all similar new characters have originated in the offspring of a single pair, which we know is not the case, *that the vast majority of similar new numerical characters both in vertebrates and invertebrates are related through similarity of ancestry, through the similarity of the tissues from which they arise, and through the similarity of their relations, forming a special kind of homology which Fürbringer has termed homomorphy.*

While different in these respects of analogy and homology there are many properties which allometrons and rectigradations as heritable characters have in common, such as the laws of growth, correlation with sex, mechanical correlation, differential ontogenetic movement, differential phyletic movement, or differential rates of evolution, continuity of origin, increasing intensity of

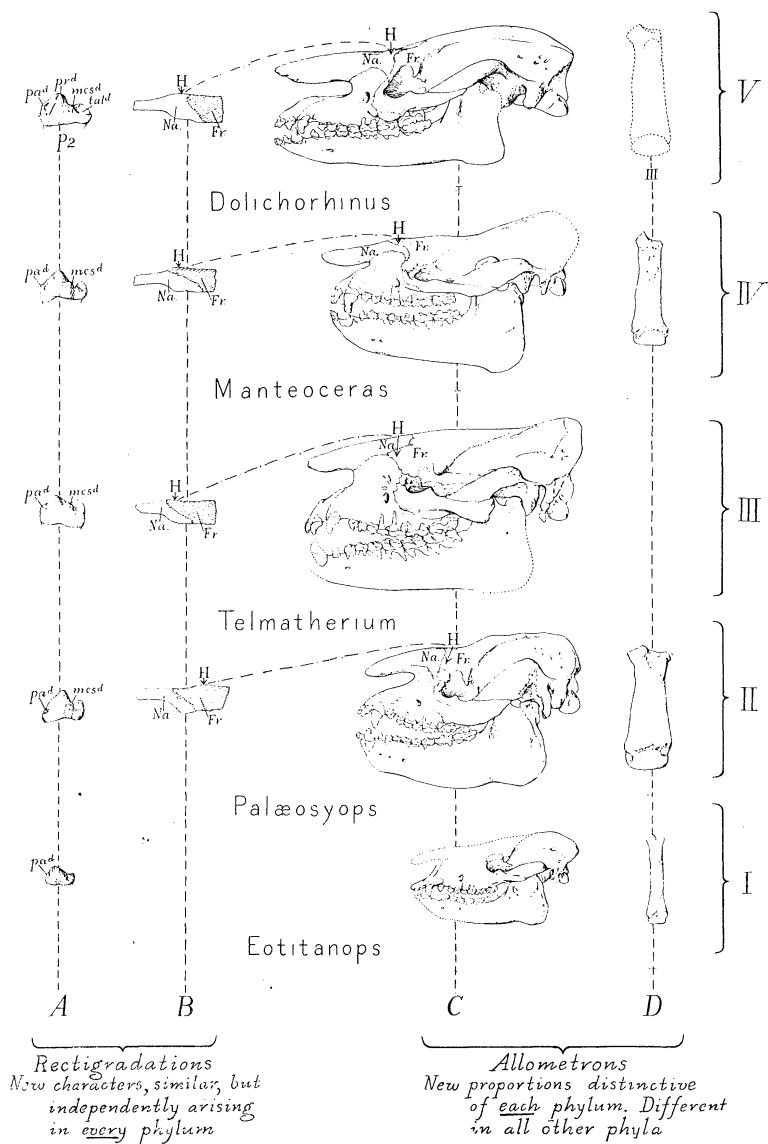


FIG. 5. The independent origin and evolution of similar numerical characters (A, B) and of dissimilar proportional characters (C, D) all arising independently in descendants of the same ancestors. Each of the five phyla (I-V) exhibits similar rectigradations (*pad*, *mesd*, *H*) and dissimilar proportions both in the skulls and metapodials.

development in successive generations. For example, a rectigradation like the hypocone may become more distinct, a change of proportion like brachycephaly may become more pronounced in successive generations. Yet there are a number of additional contrasts between the proportional and certain numerical characters, a few of which may be enumerated:

Proportional characters = *Allometrons*

Allometrons give rise to analogies, never to homologies; they are quantitative and intensive and not numerical; closely related forms give rise to different allometrons even within species; they may be induced experimentally in ontogeny; they constantly afford indices and ratios; even specific affinity may not predispose to the same allometrons; allometrons—both harmonic and disharmonic—frequently accompany changes of environment; they give rise both to convergence and to divergence.

Orthogenic numerical characters = *Rectigradations*

Rectigradations give rise to homologies, strictly speaking homomorphic structures; they are neomorphs, new outgrowths, numerically new characters; similar rectigradations may arise in all the descendants of similar ancestors at different periods of time; they always give rise to parallelism or convergence between the members of related phyla; they are comparatively infrequent phenomena; they are not known to be produced experimentally in ontogeny; they arise from minute beginnings at different points in the tissues; they adopt the characters of proportion in surrounding parts; no true rectigradations have been observed to arise *per saltum*; the closer the taxonomic affinity the more numerous the similar rectigradations.

4. *Differences of Opinion as to the Origin of New Numerical and Proportional Characters*

In my opinion, which is not shared by all my co-workers, rectigradations and allometrons are qualitatively different characters and are attributable to different combinations of causes. For example, the additional cuspules on the teeth of *Canis*, *Alopex* and *Vulpes* are typical rectigradations; they are “characters” qualitatively different from the dolichocephaly of *Vulpes* or the relative brachy-

cephaly of *Canis*. This opinion was formed in 1905 and has in my mind been established by further research.

It is, moreover, my theoretical view that rectigradations arise from some kind of germinal predisposition or prepotency or potential homology. While the "homology" or "homomorphy" uniting these new characters seem to be due to some internal hereditary kinship between the descendants of similar ancestors, their appearance is not

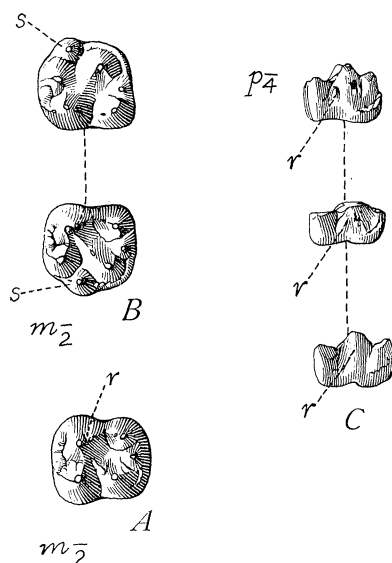


FIG. 6. Distinction between sport or mutational characters (*s*), which have no significance in the evolution of the teeth, and rectigradations (*r*), which are very important.

spontaneous, but is invoked in some way connected with similar bodily and environmental reactions which also we do not at all comprehend. For certainly there is no evidence that such "homologues" or "homomorphs" arise from similar internal perfecting tendencies or teleologic causes which operate independently of the reactions of environment and habit.

The fact that certain rectigradations appear to correspond with antecedent mechanical reactions in certain cases, such as in the cuspsules of the teeth, has led to the opinion of Cope that these bodily mechanical reactions are causative, but this opinion is completely offset by the fact

that many rectigradations occur in both vertebrates and invertebrates which are not preceded by mechanical reactions in the bodily tissues, the ornamental characteristics of the shells of molluscs, for example.

In brief, the mechanical reaction hypothesis of Lamarck and Cope fails both as to the origin of certain new rectigradations and of certain new allometrons. For example, the extremely elongated limbs of certain young quadrupeds, such as young horses and young guanocos, are proportional characters which are certainly not due to the inheritance of mechanical reactions in the adults because they are entirely different from the adult proportions.

For these various reasons I have reached the opinion that, whatever the respective causes of rectigradations and allometrons may be, they are different; that is, the occasional origin of new numerical characters and the constant changes of proportion which are going on in all organisms are due to a different series of direct causes.

This divergence into matters of opinion is, however, parenthetical. Let us now return to the observation of facts which throw light upon the properties and qualities of these least characters.

5. *Observed Differences in the Origin and Inheritance of Proportional and Numerical Characters*

Origin. The fundamental distinction between the origin of rectigradations and of allometrons is well illustrated in the six phyla, I-V, of Eocene titanotheres (Fig. 5).

It is seen that similar horn rudiments and similar cusp rudiments arise independently at different geologic times in every phylum, giving rise to a great number of new homomorphic characters. On the other hand, each phylum has its peculiar and distinctive allometrons both in the bones of the skull and of the feet. These changes of proportion are so universal and so profound that by a vast system of comparative measurements it has been ascertained that every bone of the skull, of the limbs and of the feet has its differential rate of increase and decrease. Since these characters of form and proportion are real

characters and since they affect every bone in the skeleton we discover that characters of taxonomic import may be found in every one of the small bones of the wrist and ankle joints, which while less readily measurable are of exactly the same kind of value in classification as the more conspicuous changes of proportion in the skull and in the

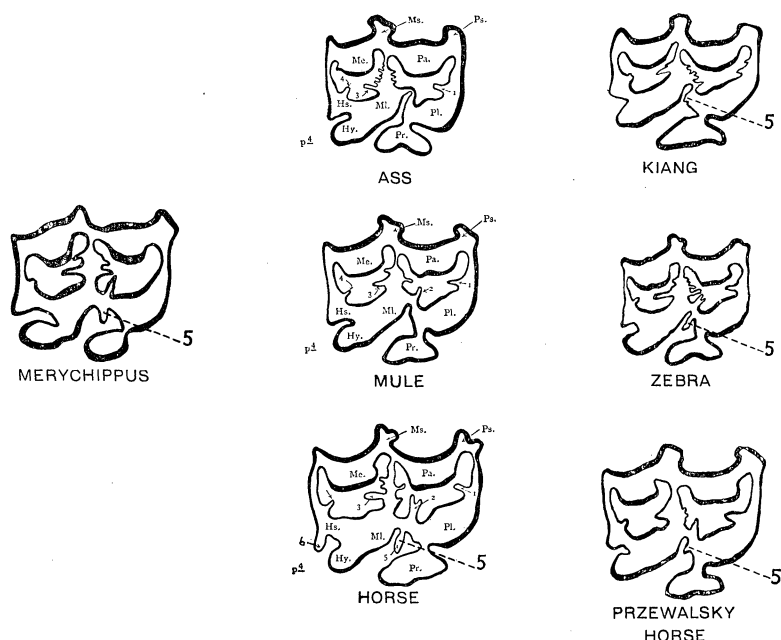


FIG. 7. The *pli caballin* (5) a typical rectigradation in the grinding teeth of different members of the family of horses. Present in the Miocene *Merychippus*, in the existing kiang, zebra, przewalsky horse, common horse; absent in the ass and the mule.

feet which Miller has used throughout in his definitions of the Carnivora. In other words a "species" may as consistently be defined by the proportion-characters of one of its carpal bones as of one of its cranial bones; such a definition would be strange and inconvenient, but it would be quite as scientific.

The rectigradations are also used in systematic definition only as soon as they become sufficiently large and conspicuous to be computed numerically. Looking up the ancient definitions of the Eocene horses by Marsh and

Cope we note in every instance that as soon as a cusp passes beyond the rudimentary stage it is apt to be observed and used in definition.

So far as we know both rectigradations and allometrons arise continuously, definitely or determinately, and so far as we have observed they arise adaptively or in an adaptive direction from the very beginning.

Inheritance. The germinal separability of the "least-characters" known as rectigradations is well illustrated in the case of the "*pli caballin*," a delicate fold of enamel

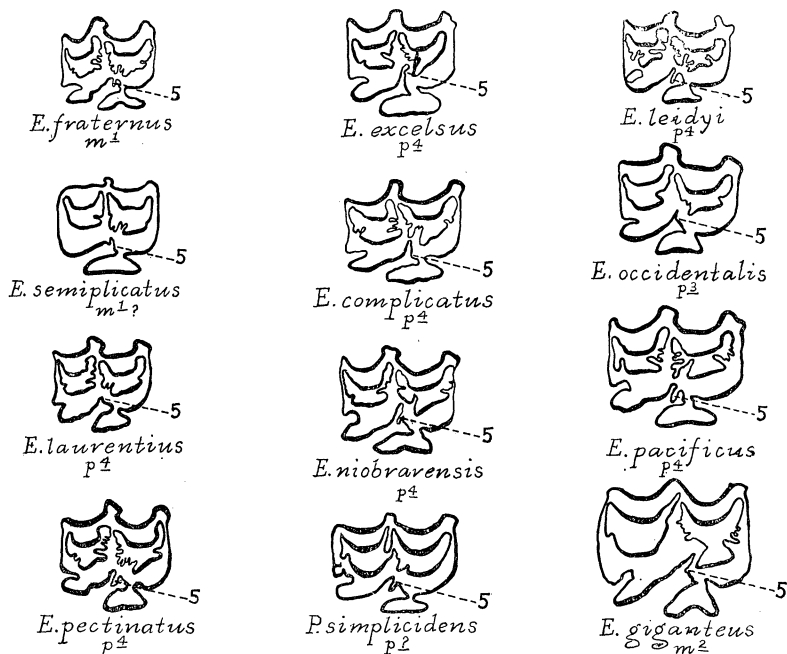


FIG. 8. The *pli caballin* (5) more or less distinctly developed in the superior grinding teeth of twelve species of the Pleistocene horses of North America. It is observed that these grinding teeth differ profoundly in the proportions of all their parts. The *pli caballin* (5) is worn off in the aged grinding tooth.

which the French systematic writers a century ago selected as a specific "character" by which the horse (*E. caballus*) could invariably be distinguished from the ass (*E. asinus*). They little knew how very ancient and stable this minute character is. We see it strongly developed in the Miocene *Merychippus*. We do not know whether it

developed gradually or suddenly within the highly varied horses of this genus. It appears (Fig. 5) more or less fully developed in all of the many known species of Pleistocene horses of America as described by Leidy, Gidley and Hay. It lies near the surface of the crown, and in much-worn teeth it disappears because the fold is seldom continued down into the lower half of the crown. It is entirely absent in the grinding teeth of the domesticated ass (*E. asinus*), yet it is present in the kiang (*E. kiang*).

The complete germinal separability of the "*pli caballin*" as a hereditary character is demonstrated by its absence in the grinders of the mule, the cross between *E. caballus* ♀ and *E. asinus* ♂; these grinders of the mule hybrid also prove that rectigradations are distinct from allometrons, because the rectigradations of the maternal horse molar are not inherited in the hybrid while the allometrons are inherited, namely, the elongated proportions of the maternal horse molar. I am preparing to investigate the grinding teeth of the hinny, the cross between the male horse and the female ass, to ascertain whether the same contrast in heredity prevails here. I suspect not because the hinny appears to have the shorter head of the ass rather than the very long horse-like head of the mule.

The germinal separability of allometrons or proportional characters of mammals is also observed, but it appears to be less complete than that of rectigradations. This is demonstrated not only in the grinding teeth but in the skull of the mule hybrid, in which the *majority* of the head proportions present the same indices as in the horse, while the *minority* of the head proportions present a blend between the indices of the horse and ass. Again in *Homo sapiens* the allometrons are in the first generation completely separated; in intermarriage of dolichocephalic and brachycephalic individuals the children do not form a blend of their parents but inherit either the pure dolichocephalic or pure brachycephalic head form. Prolonged interbreeding and intermixture between long-headed and broad-headed human races ap-

pears to break down these separable allometrons and ultimately results in blending. This may be partly due to the fact that changes of cranial proportion occur not only within the species, but within the races and sub-races of *Homo sapiens*, as witnessed in the mongoloid Indian races of North and South America. In other words, the allometrons in man are of more recent origin than in the horse and ass, which probably separated from each other as far back as the Lower Miocene. Further experiments and observations are greatly needed as to the separableness or blending of allometrons in hybrids.

As to the rapidity of evolution of proportional and numerical characters it appears that in certain lines allometrons may evolve more rapidly than rectigradations. This is seen in the titanotheres (Figs. 4, 5, 10), in which changes of proportion develop very rapidly, while the rectigradations on the grinding teeth and the rudiments of horns develop very slowly. On the other hand, in the contemporary Eocene horses the rectigradations seen in the addition of cusps develop very much more rapidly than the changes of proportion in the skull. This contrast between horses and titanotheres, however, confirms the universal law that every "character" has its differential phyletic movement as well as its differential ontogenetic movement.

That these movements are not identical is further shown by a familiar illustration. The median toes of the feet of the desert-living *Hipparion* have a much more rapid phyletic movement than the median toes in the forest-living *Hypohippus*, yet we may be sure that the limbs of the newly born foals of *Hipparion* and of *Hypohippus* were alike relatively elongated to enable these foals to accompany the mares in flight, this adaptation being secured through ontogenetic movement, or acceleration.

These differentials in the velocity of characters in their phyletic and in ontogenetic movements may afford one of several reasons why allometrons, or proportional characters are separable in hybrids, why some "unit

characters'' are dominant and others recessive. This raises the general problem of the *various causes of separability of characters in the body and in the germ*. First, it will appear that continuity or discontinuity of origin has little to do with separability in the germ.

6. Waagen's Observations on the Continuous and Orthogenic Origin of New Characters

The first paleontologist to point out the separate origin and phyletic movement of single new numerical characters as distinguished from contemporary proportional changes was Waagen in his observations on *Ammonites subradiatus*, published in 1869 (p. 23).¹⁴ His two great principles were announced as follows:

I. [The Variety.] The characters observed *in space* by botanists and zoologists to distinguish "local varieties," "geographic varieties," "varieties in space" are of variable value and of small systematic importance. They appear to be temporary. They do not reappear in the next higher geologic stratum. For these characters the long-used name "variety" will suffice.

II. [The Mutation.] In contrast to the *variety* I venture to propose a new term, "*mutation*," for the early and later phases (*formen*) of a species observed *in time*. These mutations are characters which are highly constant, although minute they surely are recognizable again, on which account far greater weight must be put on mutations. They ought to be very precisely pointed out, for mutation characters even when displayed in the most minute features are certain to reappear in the next geologic stratum. In each higher stratum they show a somewhat different appearance. Ordinarily the gradations between the mutations are the more minute as the stratum from which specimens come are the more closely connected.

An ascending series of mutations in successive geologic horizons taken together constitute Waagen's *Collectivart*, which is equivalent to the *Formenreihe* of Beyrich; it is also equivalent to the *phylum* of more modern terminology. Each mutation stage includes a number of geographic "varieties." In any given geologic stratum a

¹⁴ Waagen, W., "Die Formenreihe des *Ammonites subradiatus*. Versuch einer Paläontologischen Monographie," *Geognostisch-Paläontologische Beiträge*, Band II, Heft II, Nov. 1869, pp. 179-256 (Heft pp. 1-78), Pl. XVI-XX.

"mutation of Waagen" would appear as a Linnæan "species" when compared by an observer with contemporary mutations in other phyla; that is, each phylum may be separated from contemporaneous phyla by valid Linnæan characters.

The essence of Waagen's discovery is that when we observe the origin and evolution of single characters in time we are able to detect the *incipience of new characters and the profound hereditary phyletic movements*

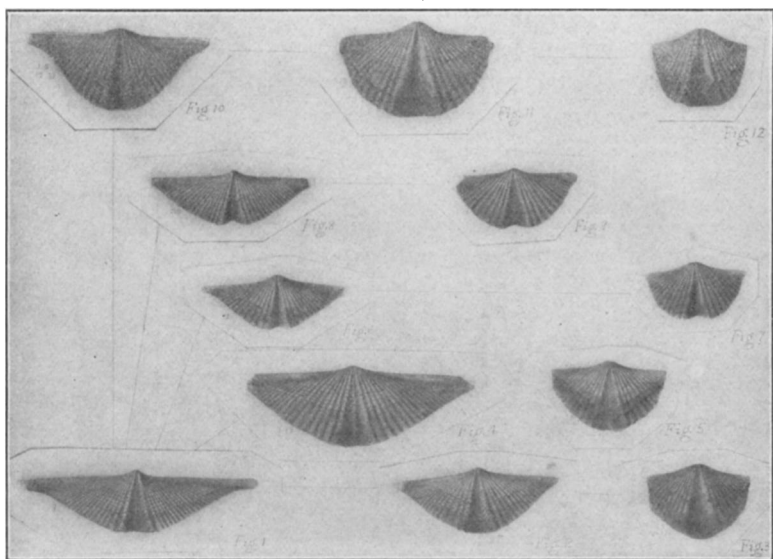


FIG. 9. "Mutations of Waagen" seen in *Spirifer mucronatus*. On horizontal lines are the geographic "varieties" differing in proportions. In vertical lines are the successive "mutations" differing in proportional and numerical characters. After Grabau.

which can not be observed by the zoologist at all. We are able, moreover, to distinguish the minute and even inconspicuous characters, which are evolving in definite directions and accumulating in successive generations, from the indefinite and transitory characters of the geographic "variety." The underlying cause of this distinction in the light of our present knowledge is that mutations denote germinal or phyletic evolution while varieties may simply denote the bodily fluctuations caused by

habit and environment. This phyletic movement was termed *Mutationsrichtung* by Neumayr.

The significance of the term mutation as defined by Waagen is to be found only in his original definition; it has been used in many different senses before and since.¹⁵ It is a *taxonomic term* for each of the minute subdivisions of a specific phylum which may be defined by certain degrees of advance in "mutation-characters" evolving continuously in definite directions. The vertebrate paleontologist Depéret in 1907 pointed out that the Waagen "mutation-characters" have this special characteristic, they are always produced in the same direction without oscillations or retarded steps. The lacunæ are so infrequent as not to interrupt the general view of the continuity. Each of the closely linked terms of any series may be designated as "ascending mutations" in rising strata. It becomes possible to recognize the intensity of the action of time.

The mutations of Waagen demonstrate five very important principles in the evolution of certain "least characters" as follows: (1) origin from inconspicuous beginnings; (2) continuity rather than discontinuity; (3) definite direction or *Mutationsrichtung* rather than indefinite or variable evolution; (4) a definite rate of phyletic movement.

These principles appear to involve a hereditary or germinal basis, a *Mutationsrichtung*, such as also appears to underlie Osborn's rectigradations.

The two kinds of characters observed by Waagen¹⁶ are also exactly similar to those observed by field zoologists and by vertebrate paleontologists, namely:

The mutation of Waagen is a *stage of advance* in the development either of numerical or of proportional characters, definable when one or more of these minute and originally unimportant characters become visible and measurable.

¹⁵ Scott, W. B., "On Variations and Mutations," *The Amer. Journ. of Science*, 3d Ser., Vol. XLVIII (Whole No. CXLVIII), Nos. 283-288, July-Dec., 1894, pp. 355-374. In this valuable paper continuous "mutation" is distinguished from indefinite "variation."

¹⁶ Waagen, *op. cit.*

It has now been made clear why these stages are recognizable and definable by the paleontologist and not by the botanist, zoologist or experimentalist.

To sum up the observations of zoologists and paleontologists with regard to the single property of the *movement of characters* in progressive organisms the following principles are observed:

All characters are in simultaneous movement; such movements are differential, each character has its own rate; some movements are ontogenic or with a velocity-relation to other characters in the same individual; others are phyletic or with a velocity-relation to similar characters in other species and genera; "least-character" movements are continuously progressive or retrogressive; certain least-characters are stationary; "least-character" movements may develop or manifest a certain direction or trend, the *Mutationsrichtung*, and thus may be cumulative to an extreme; all character movements which are cumulative in successive generations have a germinal or hereditary basis. Thus differential movement is one of the most distinctive and important properties of the "character."

This principle of continuous germinal change which appears to underlie the continuous development of visible bodily characters may prove to be in harmony with rather than in opposition to the law through which some characters appear suddenly, or by saltation. As I pointed out many years ago, there may be an apparent but not a real contrast between the "mutations of Waagen" and the "mutations of De Vries." If the former rise through continuous germinal changes and the latter rise through discontinuous germinal changes the common element in both may be the *Mutationsrichtung*, or trend of development. In Waagen's law this trend of development appears to express itself in a continuous change of visible somatic development of characters. In De Vries's observations the change is believed to be discontinuous, suddenly constituting the "mutant"

or "elementary species" which is a subspecific stage comparable to the "mutation" of Waagen.

7. *De Vries's Observations on the Discontinuous and Indefinite Origin of Characters*

The sudden origin of "characters," new, germinal, saltatory, in every direction but of sufficient value to come under the influence of selection—these are the essential features of the famous mutation hypothesis of De Vries. While I do not accept this hypothesis as a demonstrated *natural* principle like that of Waagen, the opinions of its distinguished author may be clearly set forth as compared with the observations of Waagen which have been repeatedly confirmed and verified:

(1) De Vries's "mutants" differ from the "mutations" of Waagen in appearing as fully formed "characters" and attracting our immediate attention and observation, instead of passing through a long series of initial and rudimentary stages in which they are barely discernible. (2) The "mutation-characters" observed by De Vries differ from Waagen's mutation-characters in lacking any definite or determinate direction; on the contrary, it is of their essence that they appear in any or all directions. (3) They agree, however, with the "mutation-characters" of Waagen and with the rectigradation-characters of Osborn in the fact that similar mutations may arise independently at various times in branches of the same stock, thus giving rise to homomorphic characters. (4) Let us note that the new systematic unit of De Vries, the "mutant" or "elementary species," is a *space or geographic phenomenon*; it may be contemporary with many other mutants of a single Linnæan species. (5) The "mutation-character" of De Vries is not a demonstrated equivalent to the "mutation-character" of Waagen, which is a *time or geologic phenomenon* character, observable only in a long series of generations from the same ancestor.

Now as to the present state of evidence for the saltation

hypothesis of De Vries, let us be on our guard between *fact* and *opinion*, between *natural* and *unnatural* phenomena. That the saltation of characters occurs very frequently in plants and in animals under artificial conditions there can be no doubt; yet the mass of existing evidence is from *artificial* rather than from *natural* sources.

The recent opinion of Bateson,¹⁷ who by his advocacy of discontinuity in the origin of all specific characters would be predisposed to favor the saltation theory held by De Vries, is partly negative.

The evidence for the appearance of mutations of higher order, by which new species characterized by several distinct features are created, is far less strong, and after the best study of records which I have been able to make I find myself unconvinced. . . . In so far as mutations may consist in meristic [i. e. numerical]¹⁸ changes of many kinds and in the loss of [germinal]¹⁸ factors it is unnecessary to repeat that we have obtained evidence of their frequent occurrence.

Negative conclusions have also been reached by various botanists, as, for example, Jeffrey:¹⁹

1. The Onagraceæ are largely characterized by hybrid contamination in nature.

2. This statement holds with particular force for *Oenothera lamarckiana* and other species of the genus *Oenothera*, which have served as the most important basis of the mutation hypothesis of De Vries.

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7. The mutation hypothesis of De Vries, so far as it is supported by the case of *Oenothera lamarckiana*, is invalidated.

I do not know of a single instance where a field observer in mammalogy or in paleontology has recorded a new saltation character which is known to be of any significance in the evolution of the race. On the other hand, certain field observers of birds (Beebe) and of molluscs (Crampton) are of the opinion that they have discovered proofs that certain characters arise by saltation

¹⁷ Bateson, William, "Problems of Genetics." Oxford University Press, 1913, 250 pp.

¹⁸ These [] are insertions in Bateson's text by the present author.

¹⁹ Jeffrey, Edw. C., "Some Fundamental Morphological Objections to the Mutation Theory of De Vries," THE AMER. NATURALIST, Vol. XLIX, No. 577, Jan., 1915, pp. 5-21.

in a state of nature. The vast majority of observations on the evolution of mammals either in the field (*e. g.*, Osgood) or among fossil series, where the *intergradations* have not been destroyed, points to continuity in the origin of changes of proportion. The evidence as to this continuity both in proportional and in certain numerical characters in fossil vertebrates and invertebrates is overwhelming. Saltation is, however, theoretically probable in certain numerical and meristic characters, such as supernumerary teeth and vertebræ.

8. *The Separability of Characters in the Body*

Apart from the question of the origin of new characters by saltation, the observations of De Vries and his followers furnish additional evidence of the *separability of characters* both in the body and in the germ. This law of separability in its human aspect was well expressed by Galton in 1889.²⁰

. . . We seem to inherit bit by bit, this element from one progenitor, that from another, under conditions that will be more clearly expressed as we proceed, while the several bits are themselves liable to some small change during the process of transmission. Inheritance may therefore be described as largely if not wholly "particulate," and as such it will be treated in these pages. Though this word is good English and accurately expresses its own meaning, the application now made of it will be better understood through an illustration. Thus, many of the modern buildings in Italy are historically known to have been built out of the pillaged structures of older days. Here we may observe a column or a lintel serving the same purpose for a second time, and perhaps bearing an inscription that testifies to its origin, while as to the other stones, though the mason may have chipped them here and there, and altered their shapes a little, few, if any, came direct from the quarry. This simile gives a rude though true idea of the exact meaning of Particulate Inheritance, namely, that each piece of the new structure is derived from a corresponding piece of some older one, as a lintel was derived from a lintel, a column from a column, a piece of wall from a piece of wall.

I will pursue this rough simile just one step further, which is as much as it will bear. Suppose we were building a house with second-hand materials carted from a dealer's yard, we should often find considerable portions of the same old houses to be still grouped together. Materials derived from various structures might have been moved and much shuffled together in the

²⁰ Galton, Francis, "Natural Inheritance." Svo. The Macmillan Company, 1889.

yard, yet pieces from the same source would frequently remain in juxtaposition and it may be entangled. They would lie side by side ready to be carted away at the same time and to be re-erected together anew. So in the process of transmission by inheritance, elements derived from the same ancestor are apt to appear in large groups, just as if they had clung together in the pre-embryonic stage, as perhaps they did. They form what is well expressed by the word "traits," traits of feature and character—that is to say, continuous features and not isolated points.

The observations which we have been comparing on the origin of new characters in vertebrates, invertebrates and plants certainly afford some insight into the laws of germinal change wherever we can distinguish between the true germinal expression of a character and its visible modification by ontogeny or environment. Recurring to the antithesis between the separability and the correlation of characters we may again sum up some of the many properties and qualities of single characters:

Laws of Separability

Independent germinal origin of characters, either continuous or discontinuous; independent development of similar new characters in near or remotely related descendants of the same ancestors; development of dissimilar changes of proportion in descendants of nearly related ancestors; development of similar "rectigradations," "mutations of Waagen," and "mutations of De Vries" at different times in descendants of the same ancestors; separate rate of evolution in ontogenetic movement and in phyletic movement; each character with its own origin, individuality, and rate of movement.

Laws of Correlation

Hereditary connection with the origin of similar characters in other lines of descent; strong sex correlation in the size and proportions of all characters; mechanical correlation both in the allometrons and rectigradations; compensation correlations when one character is developed by the sacrifice of another; proportional or allometric correlations where all the new characters and changes of proportion share the general form; a utility or selection correlation where one character is sufficiently strong to come directly under natural or sexual selection; adaptive, defensive and offensive correlation where groups of characters evolve to serve similar purposes.

At the present time we appear to understand the laws of separability somewhat better than the laws of correlation, for the latter are enveloped in the deepest mystery. We have not even alluded to the chemico-physical

correlations, by means of the hormones, which are observable in the field of physiology and medicine. Mechanical correlation, as where an incipient rectigradation in an upper tooth corresponds precisely with an incipient rectigradation in a lower tooth so that the upper and lower teeth evolve throughout in perfect mechanical harmony by the addition of character after character, affords one of the most vivid instances of our total ignorance of the causes underlying the origin of new characters.

9. *The Separability of "Characters" in the Germ*

The pioneer discoverer of the separability of "characters" in the germ was Gregor Mendel, who in 1865 examined seven pairs of alternating characters in hybrids of two varieties of the common pea (*Pisum sativum*). The outstanding feature of this great discovery is that the separability of the "determiners" of characters in the germ is far more sharply defined than the separability of the corresponding somatic "characters" in the visible body; as regards the "determiners" of many characters it is sharp and absolute.

A second feature of Mendel's discovery is of special significance in our present review of proportional and numerical characters in the hard parts of vertebrates because the alternative characters which Mendel experimented with were of both the proportional and the numerical kind. For example, Mendel's proportional characters of "tallness" and "dwarfness" in the pea stalk may not improperly be regarded as analogous with the alternative characters of dolichocephaly and brachycephaly of the skull of the mammal. Again, Mendel's form of the pea-seed, whether round or wrinkled, may not improperly be compared respectively with the folded or smooth condition of the enamel in the molar teeth of the ass and of the horse, which we observe is alternative in heredity. On the other hand, Mendel's definite color characters, such as his flower color, whether purple, red or white, or his seed color, whether yellow or green, have been definitely compared by experiment and found to

correspond in heredity with the coat colors of mammals.

A third great feature of Mendel's discovery is that in such alternative pairs of characters as tallness and dwarfness one may be dominant and the other recessive, following in successive generations the well-established Mendelian law.

It remains to be observed whether any of the *proportional* characters of mammals follow this law.

It remains to be observed, also, whether rectigradational characters like the "*pli caballin*" in the grinding teeth of the horse exhibit in heredity the Mendelian laws of dominance and recession. This could only be ascertained among mammals by observations on hybrids in such a family as the Bovidæ, which are fertile *inter se*,²¹ or on similar characters in the hybrids between wild natural breeds.

The discovery through experiment by zoologists and botanists that many saltation characters, such as sports and abnormalities, follow the Mendelian law of dominance and recession has led to the entirely unwarrantable assumption that only characters which are discontinuous, or of sudden origin, are sharply separable in heredity. This we have seen to be not in accord with the facts, for the *principle of separability is quite as sharply defined in certain characters which have evolved slowly and continuously as in those which have evolved suddenly.*

The special significance of recent Mendelian discov-

²¹ Bartlett, A. D., "Wild Animals in Captivity." 8vo. Chapman and Hall, Ltd. London, 1899, p. 219. "The two species of camel (*Camelus dromedarius* and *C. bactrianus*) will breed together; the llama (*Auchenia glama*) will breed with the alpaca (*A. pacos*), and the offspring are fertile. Several species of deer, when crossed, produce fertile hybrids: for instance, the Barbary deer (*Cervus barbarus*) with the red deer (*C. elaphus*), the Mexican (*C. mexicanus*) with the Virginian deer (*C. virginianus*). Several others are also recorded upon good authority. Several instances of hybrids among the carnivora are well authenticated. The lion (*Felis leo*) has bred with the tiger (*F. tigris*), the leopard (*F. leopardus*) with the jaguar (*F. onca*), the wild cat (*F. catus*) with the domestic cat (*F. domestica*)."

"Wild Beasts in the 'Zoo.'" 8vo. Chapman and Hall, Ltd. London, 1900, pp. 71-72. "Hybrid Bovine Animals. . . . In the first place, the bull

eries to the zoologist and paleontologist is that what we zoologists describe as a "single character," the horn of a sheep or of a titanotherium, for example, is probably the expression of a very large number of germinal "determiners" all of which are necessary in the germ to produce the horn. If only one of these "determiners" should change the character of the horn would change, or the horns might be lost altogether. Thus the germinal correlation of "determiners" to produce what appears as a single character to the zoologist and paleontologist is visibly represented in the bodily correlation of the horn with a very elaborate offensive and defensive mechanism including all the bony and muscular characters necessary to operate the horn effectively, as well as the psychic desires and impulses to use the horn. We thus have a vast array of internal and external, of structural and functional correlations with this single character, the horn.

10. Conception of the "Least Character"

In the beginning of this address I noted that no one has ever undertaken to define the "character."

It is very difficult if not impossible to define one of these least characters as observed in living and fossil series even when reinforced by the experimental evidence of heredity. A definition may be essayed through

Zebu (*Bos indicus*) was introduced to the cow Gayal (*Bibos frontalis*), and a female hybrid was born October 29, 1868 (*A* of pedigree). This animal (*A*) produced her first calf June 17, 1872, a second one October 16, 1873, a third one January 5, 1875, a fourth March 11, 1876, a fifth November 2, 1878; these five calves were the produce of this female hybrid Gayal with the Zebu bull. She was now introduced to the male American Bison (*Bison americanus*), and on May 21, 1881, she produced a female No. 2 (*B* of pedigree)."

"It will be seen that this animal (*B*) is the product not only of the intermixture of three well-marked species, but, according to our present definition, of three distinct genera.

"This remarkable animal, the result of the triple alliance, was last year introduced to the bull Bison, and on March 12, 1884, she produced a female (*C* of pedigree). This last individual, now eleven weeks old, is undistinguishable from a pure-bred Bison of the same age."

an enumeration of the known properties of a "least character."

As distinguished from a group of characters the properties of a "character" are its separability, its independence, its individuality, its own rate of movement ontogenetic and phyletic, its differentiation by these properties from other least characters. Its separability in heredity is shown where it can be hybridized.

From the structural or anatomic standpoint a least character is a group of cells and tissues constituting a diminutive organ or part of an organ subserving a distinct though subsidiary function. For example, the "*pliocaballin*" in the enamel of the horse's tooth or the rudimentary cuspule may be cited as least characters, for each is composed of a vast number of cells and more than one tissue, but seems to have the property of rising or falling and behaving like a unit.

11. "*Least Characters*" in Classification and Systematic Work

This "least-character" conception is of great value to the zoologist and botanist in systematic work, this conception of an individual as a colony of "characters" each with its principles of independence and its principles of correlation, germinal in origin but subject to somatic modification by environment and habit.

First, among these single characters are those observed by Waagen which accumulate until they build up into one of his "mutations." One or more such single characters compose the "mutants" of De Vries.

Second, the old but oft-confusing term "races" becomes clear; we may now understand the significance of the races of the horse, for example, the Arab, the Forest, the Steppe horse. These races are all fertile *inter se* and thus have never been defined as species although fertility and non-fertility are no more important in the distinction of species than any other "character." The characters which distinguish races are, nevertheless, often of specific value; they are either proportional or numer-

ical, because in the production of these modern races the pure ancestral forms had in their natural state evolved a very large number of allometrons as well as rectigradations and other numerical characters which have to a slight degree blended in intercourse and to a larger degree have maintained their purity and distinctness. Thus you will observe among the modern races of horses the most incongruous mixtures; an old cart horse with the head and quarters of the Forest type will gallop across a field and raise the bones of the tail perfectly erect exactly like a pure bred Arab.

Similarly a "species" is a mosaic of an infinite number of least characters in a state of movement only a few of which may be so definite and measurable as to be employed in systematic definition.

12. *Theoretical Conclusions as to "Characters" and the "Organism"*

These least characters when assembled in an organism and dominated by the principles of separability and correlation present to our fancy the picture of a vast regiment of soldiers walking in single line; each soldier possesses his own individuality and separableness from his comrades, each advances or lags behind according to his individual velocity, but each subserves the general purposes of the entire regimental line through the uniting force of training and the unseen spirit of the regiment, which represents the law of correlation.

It appears that we paleontologists have already learned much and that we have still far more to learn by the closest observation of "characters" in a state of *natural evolution*. We are on somewhat safer ground than the observer of the unnatural or hotbed evolution of characters in the artificial breeds, hybrids of animals and plants under domestication. The contrast between the excessively slow natural evolution during the past million years of the wolf, the arctic fox and the red fox, and the feverish unnatural evolution of the domestic breeds of dogs dur-

ing the last ten or twelve thousand years is extremely significant.

If the student of genetics abandons the natural and the

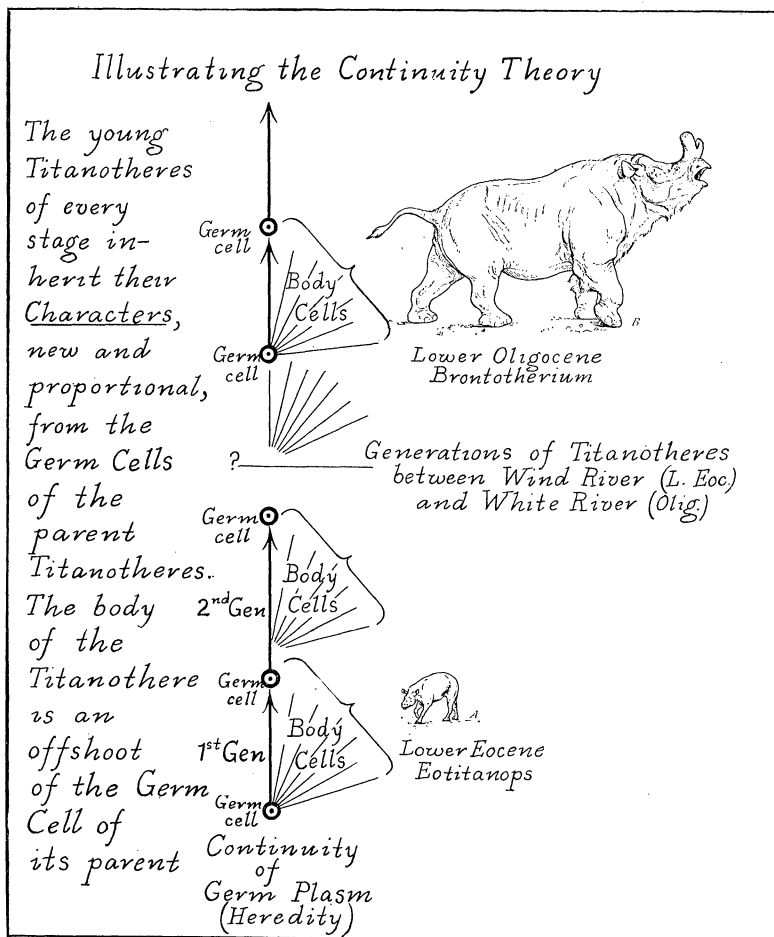


FIG. 10. Evolution by the constant addition of characters, illustrated in the descent of *Brontotherium* (B) from *Eotitanops* (A). These animals are represented to the same scale. They illustrate the constant addition of new characters in every part of the organism. Evolution in this family of quadrupeds is almost entirely by the addition of characters. Comparatively few characters degenerate or disappear.

normal for the unnatural and the abnormal and sticks solely to his seed pan and his incubator he is in danger of observing modes of origin and behavior of characters

which never have and never will occur in Nature. He may, moreover, never observe at all certain modes of origin and behavior as well as certain properties and qualities of characters which are of the most fundamental importance in relation to his particular field of heredity and hybridizing.

While twenty years of observation of the normal and the natural aspects of nature have brought the zoologist and paleontologist somewhat nearer to a conception of the modes of evolution, twenty years of continuous observation of the abnormal and unnatural have landed one of the leading experimentalists, William Bateson, in the state of skepticism and agnosticism expressed in his recent work (p. 248, italics our own):²²

The many converging lines of evidence point so clearly to the central fact of the origin of the forms of life by an evolutionary process that we are compelled to accept this deduction, *but as to almost all the essential features, whether of cause or mode, by which specific diversity has become what we perceive it to be, we have to confess an ignorance nearly total.* The transformation of masses of population by imperceptible steps guided by selection, is, as most of us now see, so inapplicable to the facts, whether of variation or of specificity, that we can only marvel both at the want of penetration displayed by the advocates of such a proposition, and at the forensic skill by which it was made to appear acceptable even for a time.

If the principle of the continuous and independent movement of each member of a vast colony of single characters is firmly established, as it appears to be through vertebrate and invertebrate paleontology, we must abandon entirely one tradition left by the master mind of Darwin which has permeated the work of all the original Darwinians and Neo-Darwinians, and which is equally strong in the mind of De Vries. Bateson has recently maintained this tradition of the origin of "species" from fortuitous saltatory characters in the following language.²³

²² Bateson, William, "Problems of Genetics." 8vo. Oxford University Press, 1913, 250 pp.

²³ *Op. cit.*, p. 248. Italics our own.

In place of this doctrine we have little teaching of a positive kind to offer. We have direct perception that new forms of life may arise sporadically, and that they differ from their progenitors quite sufficiently to pass for species. *By the success and maintenance of such sporadically arising forms, moreover, there is no reasonable doubt that innumerable strains, whether in isolation or in community with their co-derivatives, have as a fact arisen, which now pass in the lists of systematists as species.*

Broadly stated, this tradition is that evolution manifests itself suddenly in one character or group of characters; that either through individual variation such a character or group of characters is preserved and accumulated by selection, or, through saltation that such a character or group of characters suddenly arises and is imperishably fixed in the race by selection.

This is the essential feature of the Darwinian conception of evolution, namely, that an organism advances now here, now there. Such a conception is one which would naturally be fostered by observers of single living plants or animals living under unnatural conditions, or by experimentalists who observe a brief contemporary chain of organisms.

The observation of "characters" in phyla or groups of organisms advancing on a grand scale in space or in time shows that this Darwinian tradition is so partial and inadequate as to be practically false. It has been observed that every organism consists of an almost infinite number of characters, it has also been observed that the evolution of some of these characters may be so conspicuous as for a time to attract the attention of the observer or as to constitute the chief magnet for the power of selection. It has not been observed that the entire organism waits on any one of these characters. On the contrary, in all progressive organisms in which a very large number of characters are simultaneously observed it proves that every character in every part of the body is in a continuous state of movement. This is the actual result of observation and measurement.

As regards natural selection in relation to the *origin* of

characters we know nothing, we stand by the theoretic opinion that: *Selection is operating always upon the sum of all the movements, actions and reactions of characters known as the ORGANISM and upon all single characters of survival or elimination value.*

Very recent is Bateson's enunciation²⁴ of the novel hypothesis that we may have to forego the theory of addition of germinal factors or determiners and substitute a theory of variation by loss of "factors":

Paleontology affords only indirect evidence as to germinal "factors" but it offers the most positive testimony both as to evolution largely by the loss of characters, as in the case of the family of horses, and evolution largely by the addition of characters, as in the family of titanotheres displayed in Fig. 10. It is the constant addition of new somatic characters in the evolution of members of the latter family which forms the background of the present address. Whether the incessant and most impressive addition of the new somatic characters which transform *Eotitanops* into *Brontotherium* are the visible result of a subtraction of germinal "factors" may be a subject for metaphysical discussion, but is certainly without the bounds of all natural evidence. A natural view is that the invisible germ is being continuously enriched with the visible body by processes of which we can form no conception whatever.

²⁴ Bateson, Wm., "Heredity." Inaugural Address of President to The Australian Meeting of the British Association. *Nature*, Vol. 93, No. 2338, Aug. 20, 1914, pp. 635-642. (Italics our own.) "I feel no reasonable doubt that though we may have to forego a claim to variations by addition of factors, yet variation both by loss of factors and by fractionation of factors is a genuine phenomenon of contemporary nature. If, then, we have to dispense, as seems likely, with any addition from without *we must begin seriously to consider whether the course of evolution can at all reasonably be represented as an unpacking of an original complex which contained within itself the whole range of diversity which living things present.* I do not suggest that we should come to a judgment as to what is or is not probable in these respects" (p. 640).